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PROBLEM OF THE MONTICULIPOROIDEA. II

CRYPTOSTOMATA

CRYPTOSTOMATA are quite generally classed as Bryozoa, but their reference as such can still be treated as doubtful. They occupy, in fact, a central position in the disputed field of Paleozoic tabulate fossils. They are quite inseparable from Trepotomata which are most often classed as Cœlenterata. To prove them undoubtedly Bryozoa is to prove Trepotomata such also. To fail in that proof permits the latter to be classed as Tabulata, true Cœlenterata, and the Cryptostomata should then be carried with them.

Four similar groups of tabulate corals and bryozoons appear for their first geologic occurrence in the Ordovician (Lower Silurian). The Tabulata, or Alcyonarian corals, are there represented by a few but typical species, the Trepotomata are locally in great numbers, and with them are many Cryptostomata and a few Cyclostomata, the last being true Bryozoa. To the top of the Paleozoic these four groups remain associated, but there the Cryptostomata become extinct. Only in middle Mesozoic the fifth group, comprising the Chilostomata to which most living Bryozoa belong, appears at a time when even the Trepotomata have quite disappeared. The fifth and last group seems to come in suddenly, as did the others. Evidently the record is incomplete as to their origin, and the missing evidence has therefore to be supplied. Some Cryptostomata resemble in all ways the Trepotomata and these the Tabulata; others somewhat nearly simulate the Cyclostomata; and again it has been suggested¹ that they "are nothing more than Paleozoic Chilostomata," differing from these, however, in several ways. The problem centers about the Cryptostomata.

Besides this interest which the problem of phylogenetic relationship affords to the paleontologist, the geologist finds, or can

¹ See EASTMAN, Text-book of Palæontology, p. 278.

find, most of them good zone markers. They are not especially difficult to recognize in the field, their more highly specialized shapes of frond and of cell pattern making them rather easier than *Trepostomata* in that respect. Their separation into species and arrangement in taxonomic divisions is facilitated by reliable macroscopic external characters as a rule. They afford also a great variety of neat cabinet specimens, and, in short, may be recommended as worthy of close acquaintance.

The student will find a ready knowledge of the *Trepostomata* a great aid to the understanding of *Cryptostomata*. In the former group one can select a simple supposed primitive skeletal structure, from which the others can be traced with increasing complexity or differentiation. The simplest *Cryptostomata* compare with the most complex *Trepostomata*, and, while serial arrangement of differentiated types can be made, the series appear not to begin within this group but in the *Trepostomata*. It is, therefore, further convenient to begin with species of this group which most resemble those of the other, avoiding also for the present the taxonomic definitions until after representative fossil species have been studied. The newest taxonomic arrangement¹ may conveniently be referred to, however, and this one divides the sub-order into eight families. They may well be arranged in three divisions or series:

Bifoliate	Cylindrical	Fenestrate
1. <i>Ptilodictyonidæ</i>	4. <i>Arthrostylidæ</i>	6. <i>Fenestellidæ</i>
2. <i>Rhinidictyonidæ</i>	5. <i>Rhabdomesodontidæ</i>	7. <i>Acanthocladiidæ</i>
3. <i>Cystodictyonidæ</i>		8. <i>Phylloporinidæ</i>

The relation of the three groups will be discussed later, but any one might be taken first, since they are coördinate, not successive, but related each to *Trepostomata*.

Our knowledge of the *Cryptostomata* may be considered fairly complete, although species and perhaps a family remain to be discovered, while others might be eliminated. This task of completing the knowledge of the several species and genera, their fixed and variable characters, is one worthy of attention

¹ EASTMAN, *op. cit.*, p. 278.

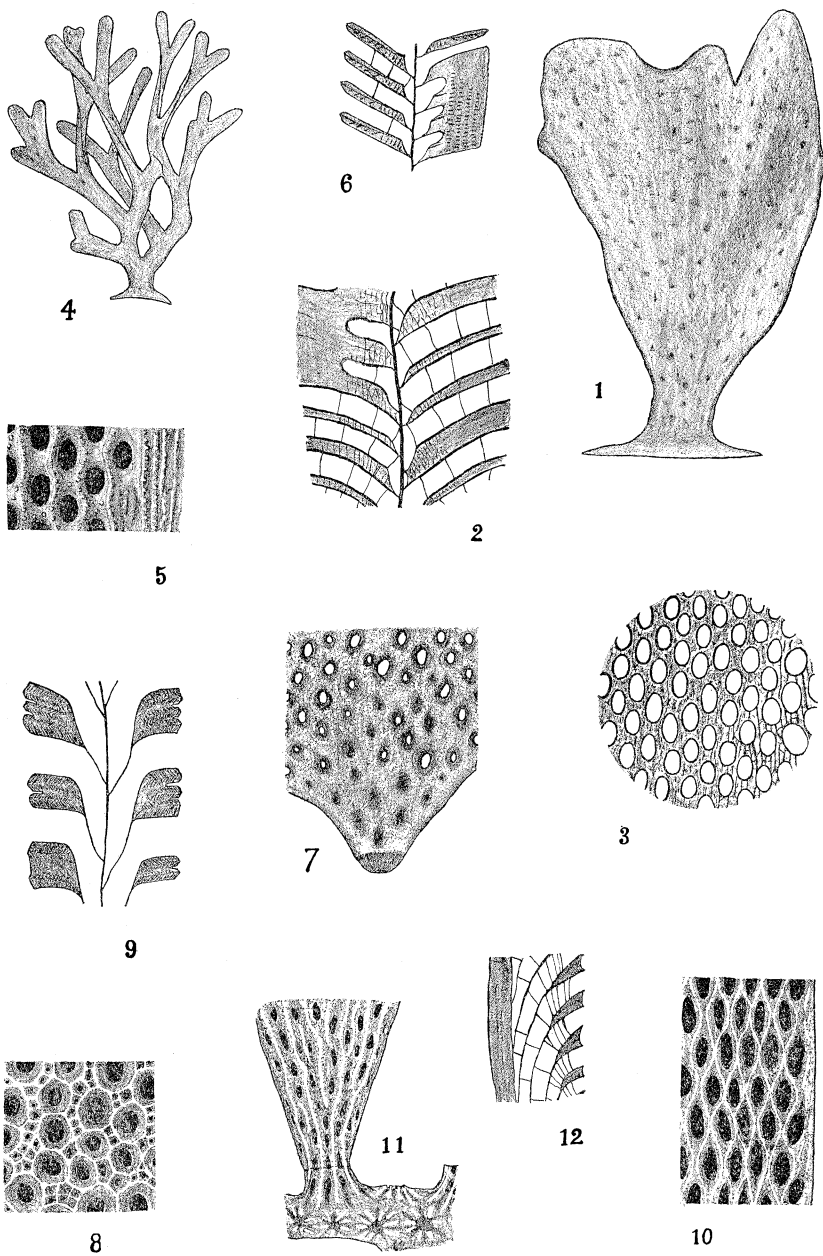
from whoever may be in favorable position to obtain the fossils. For the present the best literature is not to be taken as alike reliable on all. In extreme cases a fortuitous or abnormal character in specimens of a species may have been mistaken as grounds for a new species, and this being then peculiar may be set up as a new genus, and in turn it affects the family. Owing to the more highly specialized structures as compared to Trepostomata, Cryptostomata are, as said, somewhat easier to learn, but they are more complex to study.

For the present purpose a few common, well-known species suffice. Taking the bifoliate group first:

Pachydictya foliata Ulr. (see Plate B, Figs. 1, 2, 3) is a leaf-shaped zoarium about 50^{mm} wide and 1 to 3^{mm} thick, with auto-cells 0.3 to 0.4^{mm} in diameter growing from a median plane and opening on either side, "bifoliate." It grows at the margin, the erect frond broadening as it increases in height. The growth is not quite uniform and a lobate, undulate shape prevails. The base or broad stem of the frond is therefore the more mature, thicker part, and there the cell increase ceases first and the margin changes to a solid, sharp, or rounded narrow border. Growing margins may also appear on the face of the frond, and when large, arising near the stem, produce a so-called trifoliate frond. A basal expansion incrusts the ground, and if this was broken off a new one developed from above the broken edge. Any injury destroying part of the frond surface gave rise to a similar growth.

The basal expansion grew perigene, the frond acrogene and so that the zoarial growth and cell increase is normally at the margins only. In the frond the cells arise on either side of a median plane, or so-called mesial plate or lamina, are directed at first vertically, but as younger cells arise between, above them, they turn laterally. Thus an immature or axial and a mature or peripheral region are distinguished. The mesial lamina is built as the extreme wall at the growing edge of the frond.

The cells at the beginning, *i. e.* at the mesial lamina, are thin walled, with mesopores at their angles, but later they are separated



by mesopores, become oval and thick walled. They grow slowly in the peripheral region, to 1 or 1.5^{mm} in length with slightly increasing size. They have a few thin tabulæ, the first one in or near the axial part, the last one often at the aperture. The mesopores are small, numerous, closely tabulated, either distinct, or the tabulæ of neighboring mesopores overlapping in vesiculose way, or again in maturer stages they fill with granulose schlerenchyma. Mesopore walls are nearly always reduced so that those between mesopores are extant only vertically in zoarial direction, but mesopore corners and junction of mesopore walls to autocell wall are always partly developed. Mesopores are rarely distinct at the surface, and their space appears solid between autocells.

The arrangement of the cells is regular, alternating in vertical rows, and the surface pattern is easily used to distinguish the species. Maculæ or solid spots of filled mesopores and filled cells too, are regularly distributed over the surface and next to these the cells are a little larger sized. No cell increase is seen normally in the peripheral or mature region, not even in the maculæ.

The best specimens only show the peristome or circular wall margin papillose, and the interspaces or mesopore tabulæ granulose, or, when some walls are present, granostriate, as the maculæ and zoarial solid border usually are also. The preserved edge of a growing mesial (or median) lamina, I have not seen, but it was probably papillose. Corresponding to these structures, sections show so-called vertical or median tubuli in the midst of the double autocell wall, similar less distinct structures in the schlerenchyma of filled mesopores, and large ones in the mesial lamina. Warts and so-called tubuli on the interspaces sometimes represent reduced mesopore walls. Further details, dimensions, etc., characterizing the species may be passed over here.

One finds characters in *Pachydictya foliata* Ulr., such only as seen in Trepostomata also: bifoliate zoaria (e. g., *Ceramophylla*), occur among them also: axial and peripheral region, autocells and vesiculose mesopores (*Prosopora*, *Fistulipora*), and maculæ

differ at most in degree of accentuation. The so-called vertical or median tubuli and the mesial tubuli differ most, but are comparable directly to acanthopores. Their numbers and small size here characterizes the species and genus, however, and unites to the Rhinidictyonidæ.

The question arises again as to what interpretation should be made of the zoarium. Apparently the same interpretation is necessary in *Pachydictya foliata* as in Trepostomata. E. O. Ulrich holds that the successive loculi between autocell tabulæ were each a zoëcium, and the autocell was built by successive generations of polypites and as to median and mesial tubuli, that they were a united system of canals. One may prefer the other interpretation for the following reasons. In any case the necessary interpretation is that the skeleton or zoarium was built by a cortex of zooids over its surface, since the mesopores are outside the cells or zoëcia, and must have been built by super-zoarial secretion; and likewise the median tubuli which end not in the cells but above them. Admitting a cortex to have covered the zoarium, there is no explanation as to why successive generations instead of a single polypite should have built each cell, or how neighboring cells could have had, one four, the other three or five generations to build it. The so-called tubuli can be interpreted as the structural results of surface projections which they are really seen to be. One can explain the mesial lamina of the zoarium in this way, that, as compared to the palmate zoarium of certain Trepostomata, with long narrow axial surface and flat axial region, the bifoliate zoarium has a still more specialized, narrower axial region and the growth or axial edge being thus very narrow, the cortex bent rather than curved over it, the cell walls coinciding with the line of flexure coming to lie nearly in one plane, and to be more or less thickened. The mesial lamina is at the axial growth center, not as a germinal layer but a wall. The cell increase having ceased at full maturity at any part, the margin ceased to extend rapidly and a filled cell or "nonporiferous" margin formed.

Species of *Pachydictya*, e. g., *P. acuta* Hall, might be described

intermediate to *P. foliata* and *Rhinidictya*, but one of this genus may suffice.

Rhinidictya mutabilis Ulr., is bifoliate, with autocells 0.2^{mm} or less in diameter (Plate B, Figs. 4, 5, and 6). It begins apparently as a small thin vertical blade 1 or 2^{mm} wide, with a small basal expansion. It grows in height rapidly, increasing more or less in apical width and branching to the length of 200^{mm} or less. As the zoarium enlarges, its basal expansion widens slowly, the cell apertures filling solid. The base or oldest part of the stalk becomes thick, more or less cylindrical, and solid surfaced. The zoarial branches thicken slowly, having ceased cell increase and built solid narrow margins, the ends either meanwhile growing by cell increase or having finally ceased likewise. Further development consists only in thickening of zoarial parts.

Cell increase and greatest zoarial growth takes place only at the apices of the frond and margin of the basal expansion, as in *Pachydictya*. The width of any branch or part depends mainly on the relative growth vigor at the apex in the building of that part. The thickness depends a little on vigor of axial growth but mainly upon age and cell lengthening. At the same time the solid margin extends, so that some width is added to that of the first growth. The initial parts appear to have been small, narrow, dichotomously branching. Some individuals dwarfed or matured at this stage. Others grew long branches, 2 to 8^{mm} wide, dichotomous or palmate digitate. Just below the forks the zoarium is widest, and there a macula appears on medium width branches or a row of maculae continue down the middle on wider ones, or two to four rows on palmate parts.

The cells alternate in vertical rows. They are somewhat smaller in the initial than in the later zoarial growth stages, but as a rule the widths of the zoarium correspond to numbers of cells and cell rows. Increased number of rows is less by intercalation than by marginal addition at the side of the growing apex, and decrease is by reduction at the margin. Sometimes

a branch widened and narrowed repeatedly, but they usually grew uniformly for a great length. Branches are twisted, heliotropic.

This highly developed zoarium has equally modified cells. As in *Pachydictya* there is a mesial lamina or wall and the thin-walled, prostrate, short, axial parts of cells are in single series on either side, without mesopores, rectangular, or in part drawn out obliquely toward the zoarial margin. The peripheral cell part is sharply defined, both by obliquely outward direction and by a thick complex wall between autocell openings, which are thus a diameter or more apart. This wall comprises the cell walls which appear thin, and between them a mesopore space. In transverse and longitudinal thin sections one may see a tabulated mesopore followed by filled mesopore space, to which the cell walls are amalgamated on either side. What is most novel is a strong dark line or wall dividing the mesopore space. On the surface the mesopore space is elevated, rarely depressed, and the cell aperture rows are in furrows, separated by strong continuous longitudinal papillose ridges, and the apertures in each row by lower short transverse ones. The ridge may be double or again discontinuous, exceptionally. The ridges are the structural cause of the dark line or wall seen within the filled mesopore space. Maculæ have closer parallel ridges, and the zoarial solid margins may appear puncto-striate.

This structural development appears due to the chaining of zooids longitudinally, probably by a canal system which impressed the longitudinal furrows or troughs, causing the mesopore space to be relatively raised. These furrows end at the growing apices of the zoarium, where cells, respectively zooids, were increasing rapidly. As the growing apices became more remote from a given part or ceased, the furrows filled gradually, and a more allsided relation arose between the cells.

No mesopore calyculs have been detected and the mesopore space being confluent with the cell calyculs, and so far subordinated and fused to the autocell walls, one might conclude that

the corresponding zooids or other structure was reduced to virtually an interautozooidal cortex. Comparison with *Pachydictya*, however, shows the ridges, and corresponding internal structures to be mesopore walls in origin. The so-called tubuli seen in thin section, corresponding to surface papillæ, are then modifications of mesopore walls. The autocell walls proper have none. The so-called mesial tubuli are present. The autocell may have one or two tabulæ in the peripheral region, and at the upper angle, between the axial and peripheral cell, a small hemiseptum may appear.

Similar species to the above described as to frond, compose the genus *Stictoporella*, one of which is peculiar and further instructive:

Stictoporella cribrosa Ulr.¹ is bifoliate with branches about 2^{mm} in width, which bifurcate and anastomose rapidly, growing thus to a large broad frond with numerous oval so-called fenestrules (Plate B, Figs. 7, 8, and 9). The zoarial growth from cell increase is at the branch ends, the margins of the branches, *i. e.*, around the fenestrules very quickly becoming static as to cell increase, although with age the thickening from cell lengthening extends them, constricting or even closing the fenestrules.

Normally the downward end of the initial branch is pointed with striated solid beveled surface, which is supposed to have articulated into the crater-like socket of a striated non-celluliferous basal expansion, forming a movable joint. The wide-spreading zoarial branches coalesce with other zoaria of the same and different species so freely that this joint must have been usually immovable. When part of the zoarium died out, it was regrown by a laminar cell growth, or again fragments of a zoarium grew a new one, in which case a basal expansion unlike the first was developed, or again the fragment became the basal to a lateral fenestrated sporadic growth.

Cell increase is at the growing margin from a mesial plane, as in *Pachydictya*, but the prostrate thin-walled part of the cell is long, overlapping, so that in transverse section the axial

¹ This appears to be the *Clathropora flabellata* Hall!

region is four instead of two cells thick. As the cells turn into the peripheral region the walls thicken and distinct mesopores intercalate. The autocell has a saucer-shaped calycal at the surface and at its center a narrow cell-opening. The small cells or mesopores are either similar, especially in young fronds, or again have the cell opening and even the calycal filled solid, in which case the autocell calycals also become ill-defined, and the surface feature is that of small cell openings and broad rounded interspaces. This condition is the maturer stage. The mesopores are either few and the autocells subquadrangular or polygonal, or again mesopores are very numerous and autocells rounded. Large or small groups of mesopores forming maculae occur in broader parts of the branches, and the 0.5^{mm} wide border has mesopores only. A constricted, closed fenestrule simulates therefore a macula.

The mesopores frequently differ in size and some of them appear to become autocells, peripheral cell increase thus existing, although necessarily to a limited degree, since the peripheral cells' length is only about equal their diameter.

Thin sections reveal no tabulae in either autocell or mesopore. The thick walls are dense with a striping parallel to the surface calycal bottoms, *i. e.*, converging upwards to median wall. The mesopore openings are seen to constrict and close while their calycals fill, and then the increments of growth or striping cross them continuously, direct, or arched upward instead of downward across the mesopore space. In this case the amalgamation may be so complete that the appearance is that of one wall between autocell openings. This filling of the mesopore space contrasts with that of *Pachydictya* in that it is by laterally thickened vertical walls instead of by vertically thickened transverse tabulae. Notably the results are very similar in the end.

In closed mesopore stage the zoarial margins become solid, smooth, or striated, and in the very few zoarial basal stalks seen the autocells also are filled on the surface above the beveled zoarial articulation. Ulrich describes moreover certain closing apercula over cell apertures at the bottoms of calycals, but their

occurrence is sporadic, probably incidental to dying off of the zooids, since these structures never occur within the cell opening as tabulæ, which they should if the zooids survived their formation. This species has no warts upon the walls and no "tubuli."

Philodictya (*Escharopora*) *subrecta* Ulr. is a simple bifoliate frond, or if divided the branches do not diverge. The zoarium is sword-shaped or feather-shaped, the point or lower end articulating to a crateriform, striated basal expansion. Specimens vary from 10 to 50^{mm} long, 1 to 10^{mm} wide, and 0.5 to 1.5^{mm} thick. In fossils the basal expansion is separate from the frond, and when living they could have united by a corneous interval or the cortex alone. The frond began evidently very narrow and grew by axial, apical cell increase, the growing end widening more or less and again narrowing somewhat, according to growth vigor. Marginal cell increase near, but below the apex also occurred in some, but the older parts have a solid margin. The cells have rather short prostrate thin-walled axial part and turn more or less sharply into the peripheral direction, the walls here thickening quickly. The cells are arranged, alternating in vertical rows (Plate B, Fig 10). They are at first quadrangular, but before reaching the peripheral region become hexagonal. Here the solid interspace, or wall, thickens, so that oval or subquadrate apertures remain, these being at the bottom of calyculs which are confluent in longitudinal rows, or oblique rows in case of the cells that were added marginally. Sinuous, longridges bound the cell rows (see figure). In later growth thickening, these ridges meet alternately at the sinuosities bounding rhombic calyculs and finally change to continuous peripheries, the cell apertures becoming meanwhile somewhat larger, subhexagonal, except in the oldest zoarial part or stem where the furrows remain.

Thin sections show the cell walls completely amalgamated, the sinuous longitudinal ridges alone being evident. No tabulæ are seen, except one or two hemisepta. But the exterior of zoaria exceptionally show a few mesopore apertures, these being

in place of the furrows or again at the summit of monticules. The zoarium, if broad, is usually thickest medially, this part then having one, two, or three rows of monticules also. The thicker median part alone appears continued in the stem, which is narrow and thickened to nearly cylindrical form, tapering, ending with a beveled striated articulation area. The articulation area and supposedly the basal expansion grew *pari pasu* with the frond. In old specimens the stalk next to the articulation is solid surfaced, cell apertures having all closed over, except as to the confluent calycals or furrows.

Interpretation of this form from comparison with those described should include in the first place the suggestion that autocells which are evident are separated by completely subordinated mesopores, these being rarely evident, but really always represented in filled condition in the thick amalgamated wall. The confluence of the autocell calycals is explicable as due to the impress of a canal system which was developed strongest in vertical direction during cell increase at the apex; later an all-sided relation between zooids arising, except at the stem, where the basal expansion united. The articulation to the basal expansion shows the zoarium to have been in part non-calcareous. Again, since no pores or even "tubuli" are present, the closing up of all autocell apertures on the stem argues the cells evacuated by the zooids, except as to the calycals. The general manner of development of calycals argues the same.

The hemisepta require special mention. They have been said to have "doubtless served as supports for the movable operculum."¹ The said movable operculum is, however, unknown, and the word "doubtless" is unwarrantable. In fact, the hemisepta occur in some species beneath complete tabulæ, and in those cases they were isolated from the aperture. In *P. subrecta* no tabulæ intervene, and two interpretations may be admitted for sake of argument. The hemisepta occur one at the bottom and one at the top near the termination of the prostrate or axial cell, their position requiring no explanation

¹ Vide Text-Book of Palæontology, by C. R. EASTMAN, Vol. I, p. 279, l. 4.

except reference to some unknown particular cause if considered as accessory opercular processes. I shall add another hypothesis, viz., that they are reduced structures homologous with regular tabulæ similarly situated in other species, *e. g.*, *Pachydictya foliata* Ulr. Their position may be accounted for as related to the sharp turning of the zooid and its cell from axial to peripheral direction, and thus may be taken as evidence that the zooid evacuated the cell as it built. (See text Fig. 2, A, p. 169.)

Some smaller closely related species (*Arthropora*) are many-jointed, partly simulating, therefore, the following one. Very probably some cylindrical forms like this one should be considered as to origin as narrow bifoliate, and hence having become rounded.

Arthroclema armatum Ulr. consists of numerous small cellu-liferous jointed segments which formed a branched zoarium. Numerous primary segments form the main stem, from which lateral branches arise, these being composed of many secondary segments and bearing likewise lateral branches of tertiary segments. These hundreds of segments are each about 3^{mm} long, subcylindrical with generally six or five or four rows of cell apertures, six to ten apertures in a row. The primary segments are 1^{mm} or less in diameter, the others 0.5 and 0.3^{mm} or less.

Each primary segment has a small axial region in which the cells are prostrate, thin-walled, and angular, and a peripheral region which is thickened according to age. The small, rounded cell apertures are separated by solid, longitudinally furrowed interspace and a large prominence behind each aperture. Some of the apertures are closed by constriction near the articulation areas. The ends or articulation surfaces are solid-faced, respectively concave and convex, and the lateral articular socket, when present on a segment, is impressed in the peripheral solid wall. Thin section shows the walls thoroughly amalgamated, the peripheral region merely having striation parallel to the surface.

Secondary and tertiary segments are similar to primary ones partly developed.

A related genus, *Arthrostylus*, has the segments with four sides, one of which is without cell apertures but striated.

Rhombopora lepidendroides Meek. is strictly a cylindrical type. A small, thin basal expansion supports a long, branching, cylindrical stem about 2^{mm} in diameter. There is a central thin-walled axial region in which the polygonal cells may have one tabula, and there is a narrow, thick-walled peripheral region with narrow cell openings without tabulæ. The surface shows oval cell apertures at the center of calyces, these being arranged in transverse, vertical, and oblique rows, their margins being more or less in contact. The elevated interspace has rows of small warts, which divide the zoarial surface somewhat into rhombs, including each a calyx. Usually a second larger set of warts or acanthopores are situated at the junction of the rows. The internal wall structure corresponds, *i. e.*, the thin, dense walls of the axial region change quickly to thick in the peripheral region, with striation parallel to the calyx, interspace, and wart surfaces.

There is no distinct evidence of mesopores, but a simulation of maculæ and other characters in common with the forms of Trepodomata, genera *Batostomella*, *Eridotrypa* *Batostoma*, which they approach more closely than to other than cylindrical Cryptostomata, would indicate that the interspaces are mesopores rather than thickened autocell walls alone.

Phylloporina corticosa Ulr. belongs to the reticulate series, and has a reticulate frond and solid basal expansion (Plate B, Figs. 11 and 12). The frond is composed of so-called branches 0.5 to 1 or 2^{mm} wide, which anastomose laterally at somewhat regular intervals, producing elongate fenestrules. Each branch has cells on the obverse side, but none on the solid, smooth or striated reverse side. Thin sections show that the cells arise mesially, have a long, thin-walled, tabulated prostrate portion, then become more closely tabulated as they turn slowly into the peripheral

region. The axial cells overlap so as to be three or more deep in transverse section. The peripheral region is characterized by filled interspaces or mesopores which more or less completely separate the cells, the cell margins rising a little above the interspace at the surface. Zoarial growth as to cell increase took place only axially, *i. e.*, at the branch ends. The peripheral growth comprised thickening of the branches with cell lengthening on the obverse side and with about equally as thick, solid or rarely vesiculose increment on the reverse side, thus proving the branch to have been surrounded by a secreting cortex. Young branches usually have on the obverse a median keel, the edge of a wall or walls extending from the mesial line, and this E. O. Ulrich compares to the longitudinal ridges dividing cell rows in *Rhinidictya*. It bears a few acanthopores. An obtuse keel on the reverse produces no internal wall distinction. With age the keels disappear from the then rounded or flattened obverse and reverse sides, and the fenestrules constrict, even closing some of them. Branches are 1 to 2^{mm} thick.

The cell apertures are arranged in one or two rows on each side of the median keel, or a few more at inosculations.

The basal expansion is the key to the better understanding of this zoarium. To the description of it as "an expanded base," the following is added from specimens at hand: Basal expansion thin, incrusting, about 2 or 3^{cm} in diameter, the marginal or younger part bearing stellate monticules like those of *Stellipora* (*Constellaria*), *i. e.*, a central depressed macula with six to twelve rays, between which are as many sloping ridges of autocells. These monticules or stars are about 3^{mm} in diameter. The rest of the expansion is crowded with young stars between larger older ones of various sizes. It appears that the stars increase in size by addition of a few ridges, all of the ridges elevating rapidly at their proximate ends. When about 1^{mm} high they begin to anastomose, and they continue to grow and elongate upward, anastomosing and branching, whence arises the reticulate funnel-shaped frond, with cell apertures turned to the outside and a solid, striate surface on the inner side; the obverse side of the

branches arising from the celluliferous ridges of the monticule, the reverse solid surface continuing from the central macula, which has become solid or coarsely vesiculose, succeeding distinct mesopores, and forms the bottom of the funnel. The median keel of the obverse side is, again, the continuation of that of the ridge in the monticule stage, the same as appears in the ridges of stars on *Stellipora*. The arrangement of the cells on the branches originated likewise in that of the stars. The basal expansion bears one largest frond, two to five smaller ones, and several monticules of various degrees. The internal structure of the basal is more similar to *Stellipora* than to that of the frond or reticulate part of *Phylloporina*.

The grown funnels must have crowded each other, and in fact fossils evince irregular shape in their later stages. Some evidently met accident, since specimens occur in which a new growth arises from the broken edge of an older piece and in a new direction. Also, a secondary basal lamina may develop from the poriferous side of a fragment, bearing new somewhat regular stars or monticules. A fragment may convert itself into a single large monticule or new basal, and other variations occur.

The long cells with many tabulæ in *Phylloporina* are remarkably like those of Trepotomata. The basal expansion like a *Stellipora* and the development of the reticulate funnels from monticules suggests relationship with Trepotomata and not with bifoliate Cryptostomata. There is not then any relation between the *Stictoporella cribrosa* type of anastomosing branches and the similarly anastomosing parts of *Phylloporina*, which might better be called bars than branches to distinguish them.

Other truly reticulate forms probably derived from *Phylloporina* as E. O. Ulrich suggests.¹

Septopora biserialis (Swal.) has branches or bars 0.8 to 0.3^{mm} wide, dividing laterally, and united at intervals by transverse processes called dissepiments, rather than anastomosing,

¹ EASTMAN, op. cit., p. 281.

the whole forming a fenestrated frond with primary branches or bars arising from an irregular basal attachment, and from these a little narrower, parallel to slightly radiating ones. The fenestrules are rather wider than the bars; ten bars occur in 1^{cm}. They have celluliferous obverse side and solid reverse, the latter on the outer or under side of the zoarium and forming the basal expansion and sometimes rootlike anchors at intervals above it. From the base a more or less funnel-shaped stalk supports the large frond on one side.

The cell apertures are about 0.13^{mm} in diameter and on the bars are arranged in two rows, separated by a thin median ridge which bears more or less prominent small warts or acanthopores. The dissepiments have distributed cell apertures only.

The internal structure seen by thin sections consists of short prostrate thin-walled axial cells arising mesially, turning sharply into the peripheral region where they become surrounded by interstitial solid deposit. Thus the cells have the appearance of being thin walled "enclosed in a calcareous crust," since the mesopore spaces on the obverse and the equally thick solid deposit on the reverse, surround the cells. There is a median wall or structure corresponding to the median ridge. The reverse is longitudinally striated at first, later nearly smooth, and its internal structure corresponds thereto. Further, it has been claimed that the solid deposit on the obverse and reverse had small vertical pores ending in minute warts at the surface, but that the dim structures so interpreted were open tubes may well be doubted. Another feature, the so-called dimorphic pores (cells), arise in the solid deposit of the reverse and obverse, are somewhat smaller than the regular cells but at the surface end with slightly elevated peristome like these. They are not to be wondered at, since they arise in what is homologous to mesopore space in, for example *Stellipora* or *Stictoporella*, and may be taken as evidence that peripheral cell increase had not wholly disappeared. The cells have no tabulæ, but sometimes a hemiseptum.

The dissepiments in this zoarium are comparable both to

drawn out inosculation from which they may have arisen and to side branches to which they are tending. The relation of obverse and reverse of the frond is a little strange, since they are reversed as compared to *Phylloporina*, the basal expansion also being unlike in that genus; differences which I cannot explain, but yet are of small import since closely related genera as *Fenestella* and *Semicosmium* differ in just that way. I feel not assured that the primary basal expansion is known except in *Phylloporina corticosa* Ulr.

DISCUSSION OF CRYPTOSTOMATA.

These described species may suffice to represent the Cryptostomata. The species of *Pachydictya* and *Rhinidictya* are of the Rhinidictyonidæ; *Stictoporella* and *Ptilodictya* of the Ptilodictyonidæ; nothing especially different is seen in the Cystodictyonidæ except sometimes a lunarium like that in the Trepostomata; *Rhombopora* is of the Rhabdomesodontidæ; *Arthroclema* of Arthrostylidæ; *Phylloporina* of Phylloporinidæ; *Septopora* of Acanthocladiidæ; and the Fenestellidæ are merely distinguished from the latter by having dissepiments without cell apertures on them. In these all, and those which they are taken to represent, the growth is acrogene and cell increase is almost all axial. Axial and peripheral regions are sharply defined, cells short, and mesopores filled more or less solid.

The Cryptostomata differ in degree of specialization of structures rather than in kind from the Trepostomata. In fact, they are arbitrarily divided in all respects. The defined axial and peripheral regions of zoarium appearing to arise in Trepostomata are merely as strongly to stronger developed in Cryptostomata. So also are the long, tabulated cells changing to shorter, with or without tabulæ and so-called hemiphrams or hemisepta. Peripheral cell increase is only reduced to nearer the minimum. The mesopores begun apparently as young cells in Trepostomata and developing to subordinate special structures or vesiculose to solid interstitial filling, are vesiculose to solid in Cryptostomata. Monticules ranging to the extreme

from called maculæ in the former are represented by maculæ in the latter. Indeed, sharply defined peripheral region, short cells, reduction of tabulæ, hemiphrams, filled vesiculose or solid mesopores, and solid maculæ, so-called acanthopores, and mesial lamina, lunarium, etc., are found in highly specialized Trepostomata of the Fistuliporoid type.

There is no character in Cryptostomata that distinguishes them all from Trepostomata. The former comprises essentially certain families of highly modified zoaria related to Fistuliporidae of Trepostomata. They are not a single branch from these, but three or more, as seen when examples like *Pachydictya*, *Rhombo-pora*, and *Phylloporina* are compared. The genera named are the Cryptostomata, which are scarcely separable, if at all, from Trepostomata, but are not related one to the other as closely as to Trepostomata. They compare back to *Cramophylla*, *Eridotrypa* and *Stellipora* respectively, which belong to three different recognized families of *Trepostomata*. They belong to more than distinct families, to three divisions of Cryptostomata, the frondiferous, cylindrical, and reticulate respectively. The highest differentiated Cryptostomata, also, for example, *Philodictya* and *Fenestella* unite to not the same Trepostomata-like Cryptostomata. The question should be rather on the propriety of dividing the Monticuliporoidea at all than on the probability of Cryptostomata and Trepostomata belonging to different phyla.

As to the interpretation of the zoarium of Cryptostomata, the entire skeleton, excepting the under side of the basal expansion, was covered by some kind of cortex uniting the zooids, as proved by deposits of superimposed laminæ in intercellular spaces, on solid margins, and on the reverse surfaces. The zooids built and evacuated the cells, resting more upon than in them at maturity, as proved by tabulæ close to the aperture, by closed-up autocells, as in the stem of bifoliate zoaria, and by the building of skeleton exclusively at its outer surface. Subordinated zooids, in some degree of development, were always present, since mesopore spaces, distinct or filled, are always present in the peripheral region. Solid maculæ, solid zoarial

margins, and solid obverse of reticulate ones are mesopore areas being seen sometimes as such (*e.g.*, *Stictoporella*, *Phylloporina pars*, *Semicosmium*), and are probably all really maculæ covered by subordinated zooids, or at least a cortex. Longitudinal median ridges and walls arise variously. Again, in jointed forms (*Psilodictya*, *Arthropora*, *et al.*) part of the skeleton was not calcareous. These show reduction from the entirely calcified zoarium, and also the filling up of mesopores and some autocells might be readily interpreted as due to leveling down of division walls between zooids: a process of reducing thin-walled cell mass to a solid axis within a living cortex.

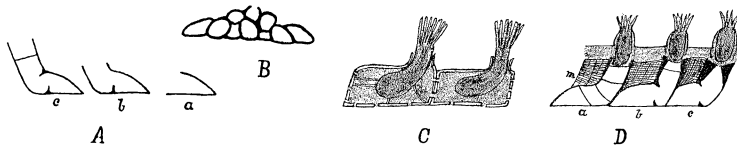
A quite different interpretation from that just given is expressed in the current definitions of Cryptostomata. Vine¹ defined them, "Zoëcia tubular, subtubular, in section slightly angular. Orifice of cell surrounded by vestibule, concealed." He does not speak of tabulæ, mesopores, acanthopores, etc., and only later knowledge, especially by E. O. Ulrich, has changed the definition, adding to *vestibule*, "which may be intersected by straight diaphragms or hemisepta owing to superimposition of layers of polypides," "surrounded by vesicular tissue or solid calcareous deposit." Vine, having in mind such as *Septopora* and *Psilodictya* without tabulæ, seems to consider the cell as a permanently occupied zoëcium; Ulrich includes the richly tabulated *Pachydictya*, *Phylloporina*, etc., and speaks therefore of superimposition of polypides or zoëcia. More direct interpretation would indicate each cell to have been gradually built and evacuated by one zooid, as argued in the preceding pages. For corresponding explanation of hemisepta see text, p. 161.

The separation of Cryptostomata from Trepostomata is scarcely tenable, and they may be discussed together. The zoarium of Cryptostomata is merely the more differentiated, the simplest Trepostomata and the typical Cryptostomata being extremes in the same line. This developmental series might well be compared to the reduction of thin-celled Tabulate corals

¹ Brit. Assn. Rep., 1883, p. 184.

to a solid axis,¹ details of which may be omitted here, since there is no character in Cryptostomata as also in Trepustomata negative to supposed relation of Monticuliporoidea to Tabulate corals as already discussed, unless, as said, their relation to Bryozoa can be proved.

In comparing to Cylostomata to which Cryptostomata have been sometimes referred, *Stomatopora* and *Berenicea* come first into consideration. Vine referred them to Cryptostomata in



AFFINITIES OF MONTICULIPOROIDEA.

FIG. 2. Diagrams showing: *A*. Interpreted origin of inferior and superior hemiseptum. *a*, axial cell stage; *b*, turning stage; *c*, peripheral stage, hemisepta remaining at points where the relation of zooid and its cell changed most. *B*. *Proboscina minnesotensis* Ulr., transverse section. $\times 40$. *C*. Relation of zooids of Bryozoa to their cells, for comparison with *D*, the interpreted relation in Cryptostomata. *a*, tabulated cell as in *Pachydictya*; *b*, cell with hemisepta as in *Philodictya*; *c*, cell closed by wall-thickening as in same.

fact. These genera comprise essentially the Paleozoic Cyclostomata, and range from Ordovician to Recent times. *Stomatopora* (e. g., *S. inflata* H.) forms branching single series of club-shaped prostrate free cells, each arising from under the anterior, larger end of the preceding one, and having a small circular aperture on the anterior upper side. Its walls are said to be minutely porous if well preserved. *Stomatopora* is not comparable to any of the Monticuliporoidea, but is a key to species called *Proboscina* or *Berenicea*.

Proboscina minnesotensis (Ulr.) forms two, three, or more series of prostrate cells, each arising from under the anterior of the preceding cell of its series. The anterior end is drawn out upwards, making a vestibule, as it is called, bearing the round aperture. The cells appear superficially as immersed in a band of stereom, but thin sections show only compacted, thin-walled

¹ *Pachypora*, *Corallium*, etc., see Neues Jarb., Beilb. X, p. 306-312.

cells (text Fig. 2, *B*), the alternating apertural ends being rounded, the other cells at that point being appressed, angular. The walls are poorly preserved as compared to fossil brachiopods and corals upon which they have grown, but very probably the basal side of the cell only was porous. Sometimes the bands or branches become very wide, thus approaching nearly *Berenicea* proper, in which perigene growth, like that of incrusting monticuliporoids is simulated. Since *Stomatopora* and *Berenicea* include also Recent species, their position as Bryozoa is established. The serial relation of other Cyclostomata and the rather similar zoaria of Chilostomata are further well shown in handbooks, and will not be discussed here.

In comparing *Berenicea*, including *Proboscina*, one at once notes that there are no tabulæ, no monticules or maculæ, no mesopores, no thick walled region, that the apertural vestibules are free and cell walls perforate. Monticuliporoid cells have imperforate walls. Further, all monomorphic monticuliporoids are again different, having without exception apertures of cells crowded together. Dimorphic forms with tabulæ are also to be excluded, while dimorphic, short celled, non-tabulate forms may be admitted to closer comparison. In fact, such as *Protocrasina* (Eastman, *op. cit.*, p. 262, Fig. 417) appears to be, might be bryozoon or monticuliporoid as to its outward aspect, the nature of its walls as poriferous, thin, or dense, thick, being the determining difference. But the comparison requires the Cyclostomata to be viewed as derived from highest specialized Monticuliporoidea, the dense autocell walls of these to be explained as having become porous in *Berenicea*, *et. al.*, and the thick, solid mesopore spaces reduced to a minimum, and thus at once a weak chain of hypotheses or an arbitrary definition is required to unite the nearest Bryozoon, *Berenicea*, to Monticuliporoidea.

Other Cyclostomata differing from *Berenicea* in changing the prostrate growth into bifoliate, acrogene, or massive form, and the cell apertures and vestibules from free to more or less in contact as in *Osculipora*, *Aspendisia*, etc. (Eastman, *op. cit.*, pp. 264-265), resemble thereby such monticuliporoids as *Stellipora*,

Septopora, etc., but only superficially. The Cerioporidæ (*op. cit.*, p. 266) most resembling Trepotomata have porous walls and are in the second place not well determined. If viewed as derived from Trepotomata the walls being assumed as having become porous—an admissible hypothesis—this hypothesis requires a reverse view of the evolution of Cyclostomata from the first one, *i. e.*, that the long tabulated cell, not the short open one, is the more primitive in Bryozoa.

The same differences disunite Chilostomata as Cyclostomata from the Monticuliporoidea, where also their outward appearance is similar, as for example *Retopora* (*op. cit.*, p. 289) and *Septopora*.

The greatest importance rests on the interpretation of the zooid's position with reference to the cell. In Bryozoa the zooid inhabits closely the cell. In order to refer Monticuliporoidea to Bryozoa it appears essential that the zooid be considered as occupying the cell and Vine has so interpreted in his definition of Cryptostomata, as said. In cells without tabulæ of some species the interpretation might appear logical (*e. g.*, *Ptilodictya*, except on the stem) but other species have tabulæ (*e. g.*, *Phylloporina*), whence the interpretation of superimposition of zoecia and of zooids. This interpretation then unfortunately assumes that which most requires proof. If there is anything clear in Monticuliporoidea it is that the cell is the unit structurally in every zoarium, that loculi between successive tabulæ can not be coördinated as such units because of inconstancy alone. They vary in length and breadth ratio from 1×10 to 10×1 and more, in the same zoarium. The interpretation of loculi as zoecia precludes all uniformity of size and shape of zoecium. In fact, the loculi are not described as structurally units in any species—but the cell. In the definition of orders only the successive loculi have been called zoecia, an interpretation that is simply not supported by any evidence from the zoarial structure.

Interpreting the cell, not its loculi, as the zoecium a great difference is at once evident between Bryozoa (text Fig. 2, *C*) and Cryptostomata (Fig. 2, *D*) and Monticuliporoidea in general in the position of the zooid—a matter of greater importance

than tabulæ, hemisepta, acanthopores, communication pores, etc. Moreover, tabulæ characterize the Monticuliporoidea and true pores the Bryozoa. One cannot assert that no bryozoans have tabulæ but they probably do not. The superimposition of cells frequently occurs in monticuliporoids and in bryozoans, but forms a recognizably distinct structure from that of the tabulated cell proper. One finds, again, many descriptions of pores in Monticuliporoidea but none recognizably like those in Bryozoa, which run direct, transverse, through the cell wall as communication pores. The supposed pores parallel the cell walls and do not end in the cell, and if they were demonstrably pores, their difference would rather serve to separate the group from true Bryozoa. They are not pores in most cases. In case of the reticulate cryptostomata one might not wish to deny that pores could exist, but yet their existence is notably only in the mesopore space or outside the autocell wall, and might be interpreted like the minute porosity of some corals (*Tubipora*) due to living cells remaining in the stereom, rather than as canals.

SUMMARY

Briefly reviewed the Monticuliporoid zoarium consists, in the first instance of monomorphic tabulated cells, differing from the extinct *Chaetetes* corals in the cell increase being less often by fission than budding. In the second instance, the young closely tabulated cells develop with a retarded or mesopore stage preceding full size growth. In the third, many cells appear to be permanently mesopores, autocells however arising from mesopores. Some autocells displace several mesopores in their rapid growth expansion and the mesopores are either distinct or their bounding walls imperfect and tabulæ vesiculose. This development and its minor features is paralleled in living and fossil Alcyonarian Tabulate compound celled corals. In the fourth instance the cells are shortened, and the mesopores or interstitial space filled solid either by superimposed tabulæ or by thickened bounding walls: cells with few or no tabulæ or filled: Cryptostomata.

There is an accompanying differentiation from uniformity in the first instance to marked axial and peripheral region of the cell in the fourth and other characters incidental therewith. But all things considered the monticules and their special form maculæ, are all that separate the Monticuliporoidea from other Tabulate (Alcyonarin) corals, but apparently not from certain living Alcyonaria, which have possibly descended from them.

As to Bryozoa, two hypothetical comparisons with Monticuliporoidea are to be considered. First, the Cerioporidae including *Heteropora*, may be Bryozoa derived from Monticuliporoidea in the first instance just mentioned, the solid wall having become porous with transverse canals. Secondly, Berenicea and other Bryozoons with more or less free vestibules might have derived from the fourth instance, being then a fifth stage or instance, the mesopore solid filling having reduced to nothing and imperforate cells walls having become perforate.

The Monticuliporoidea are difficult to separate from corals in two concordant instances. In two instances in which their structures nearest approach the Bryozoa, they separate easily or rather are difficult to unite with them, and of these instances the one probably negatives the other.

EXPLANATION OF PLATE B.

- FIG. 1. *Pachydictya foliata*, frond natural size.
FIG. 2. *Pachydictya foliata*, longitudinal section. $\times 10$.
FIG. 3. *Pachydictya foliata*, tangential section. $\times 10$, showing cell pattern.
FIG. 4. *Rhinidictya mutabilis*, frond of an undersized individual.
FIG. 5. *Rhinidictya mutabilis*, part of surface. $\times 20$, after Ulrich.
FIG. 6. *Rhinidictya mutabilis*, longitudinal section. $\times 10$.
FIG. 7. *Stictoporella cribrosa*, lower part of frond with articulation.
FIG. 8. *Stictoporella cribrosa*, surface. $\times 20$.
FIG. 9. *Stictoporella cribrosa*, longitudinal section. $\times 20$.
FIG. 10. *Ptilodictya subrecta*, surface. $\times 20$ showing zoarial margin.
FIG. 11. *Phylloporina corticosa*, part of basal expansion and one frond. $\times 2$.
FIG. 12. *Phylloporina corticosa*, longitudinal section. $\times 20$.

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